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THE GALL OF THE MONTEREY PINE.

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ONE species of pine, the Monterey pine,[1] which is especially abundant in the arboretum of the Leland Stanford Junior University, has recently been so seriously affected by a gall that the beauty of a great number of the trees has been greatly impaired, and their total destruction made probable. The gall is caused, as was first observed by Mr. W. A. Snow,[2] by larvæ of a gallfly belonging to the family Cecedomyiidæ.

The gall consists of a malformation of the leaves and leaf bases. The galled leaves vary in length from .5 to 1.5 cm., and their bases are so badly swollen that the leaves are often pear-shaped. The larvæ live in pockets in the swollen leaf bases. The gall occurs on the youngest leaves, and for that reason leaves containing larvæ are to be looked for at the tips of the branches. Where the same branches have been galled several successive seasons their tips appear as if closely clipped and look like great bottle brushes. The galled leaves do not remain so long on the tree as the normal ones.

If one of the galled leaves be examined the autumn after it has been stung, it will be found to contain in its base four or more larvæ. These are without biting mouth-parts, but they are none the less completely enclosed by plant tissues. It was to learn, primarily, how the larvæ got inside of the leaf base, and also to trace the immediate cause of the hypertrophy, that this study was undertaken. To these were added, in the course of the investigation, other questions of physiological interest.

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[1] *Pinus radiata* D. Don., *Trans. Linnæan Soc.*, vol. xvii (1836), p. 441; formerly known as *P. insignis* Loudon, *Arb. Brit.*, vol. iv (1838), pp. 2265, f., 2170–2172.

[2] This study was taken up with Mr. Snow, since deceased, and subsequently carried on by Miss Helen Mills. *The Entomological News*, vol. xi (1900), p. 489.

In dealing with the inner morphology of the galled leaf it was not thought necessary for the purpose of this paper to follow minutely all of the changes in the plant tissues during the development of the gall, but rather to observe the conditions of the tissues in well-marked stages of growth, and contrast them with each other and with the conditions in normal leaves.

I.

In the middle of February the young shoot representing the season's growth of the branch is about 3 cm. long and consists of a central axis covered closely with leaf bundles, or fascicles. There are about seventy leaf bundles, or fascicles, to each young shoot. Each bundle is composed of a short secondary branch bearing three leaves, or "needles," which are closely and completely enwrapped by several protective scales. The whole springs from the axil of the primary leaf (Fig. 1). Early in the season each primary leaf completely covers its leaf bundle, but by the middle of February the leaves begin to grow appreciably and soon stretch up above the tip of the primary leaf. At the tip of each young shoot there will be fascicles hidden by the primary leaves, while at the base of the same shoot these bundles may be twice as long as the primary leaves, and between tip and base an intermediate condition may be found. At the time the gallfly is active the majority of leaf bundles are about 2 mm. in length. The length of the leaf bundle in relation to that of the subtending primary leaf and to that of the ovipositor is of great importance in connection with the successful deposition of the eggs.

To learn in what part the eggs were placed, the young shoots were examined in February, during the activity of the gallfly. The eggs were found deposited in masses on the outside of the young shoot. They were placed, also, in great numbers between the leaf fascicles or between the primary leaves and the fascicles they subtend (Fig. 1, *B*), and it was thought at the time that the fly did not deposit the eggs in any other parts. The young shoots were examined to see if some substance, such as formic acid, were not deposited by the fly at the time the eggs were laid, which might in this case, as in others, stimulate the plant tissues to abnormal growth and thus bring about the gall. The cells, however, adjacent to the masses of eggs did not show the slightest discoloration or shrinkage of contents, nor did they in any other way that could be discovered indicate that substances were deposited which might stimulate or affect the plant tissues. All of the eggs which were placed on the outside of the young shoots disappeared on the first of March. A closer examination of the leaf bundles showed that, in addition to the great numbers of eggs placed on their surfaces, the fly also placed some inside of them. The eggs which were deposited within the leaf fascicles were in much smaller masses than those on the outside. The number of eggs in these masses did not, in any case observed, exceed six. They were found in three positions. Some eggs were between the enwrapping scales, others inside of them but near the tips of the leaves, and still others within and at the bases of the inner scales (Fig. 2, *A*, *B*). These different positions of the eggs might not all be met with in any one bundle, but they were of frequent occurrence. In those cases where the eggs were placed between the scales, and also where they were deposited

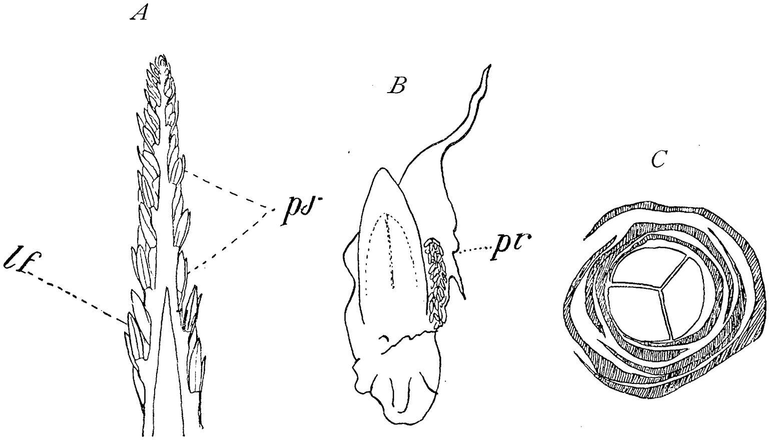

Fig. 1.—*A*, young shoot with leaf fascicles (*lf*) and primary leaves (*pj*). × 2. *B*, dorsal view of a young leaf fascicle with its primary leaf (*pr*) attached, showing a mass of eggs between the two. × *circa* 10. *C*, transverse section of the same with the protecting scales. × *circa* 16.

within the scales but near the tip of the leaf, they did not give rise to larvæ that matured, because, as will be shown later, the young larvæ were not in contact with living tissue which could give them nourishment. The larvæ take their food only by absorption through the surface of the body. This makes it essential for them to be in contact with living cells, from which the necessary food matters can be abstracted. This condition, namely, that the larvæ must be in physical contact with tissues which will give them food, is fully realized only when the eggs from which they develop are placed at the bases of the inner scales. It is consequently necessary that the distance from the tip of the needles, or in other words the length of the leaves, be approximately the same as the length of the ovipositor of the fly, for only in this way can the eggs be so placed that the larvæ which result from them will live. This exacting condition we find is complied with by most of the leaf bundles of the Monterey pine during the month of February, or during the season of the gallfly's activity.

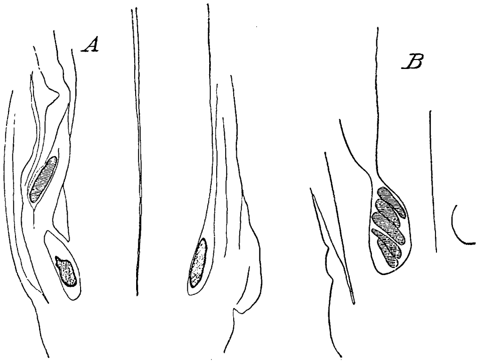

FIG. 2.—*A*, longitudinal section of a leaf fascicle with eggs placed at the base of the leaves and of the inner protecting scales ; one egg is also shown between the scales. × 28½. *B*, longitudinal section showing a mass of eggs at the base of the leaf. × 28½.

II.

All of the young leaves grow rapidly in length during the month of March, and the first week in April most of them are approximately 1 cm. long ; thus, they have increased about five times in length in somewhat over four weeks (Fig. 3). Up to the first of April there is no apparent difference between the normal and the galled leaves ; from this time on, however, the difference in length and diameter between the affected and the normal leaf bundles, or fascicles, is increasingly marked. By the first of May the normal leaf bundles are about 3 cm. long, and the galled ones from 1 to 1.5 cm. in length. In addition to the difference in length, the bases of the latter are much swollen, and many of the leaves cease to grow in length, although the diameter of their bases continues to increase until autumn (Fig. 4).

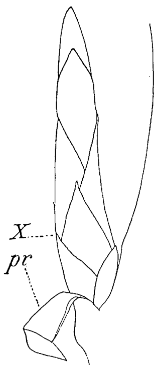

FIG. 3. — Showing the first indication of the hypertrophy at *X*. March 16. × 4.

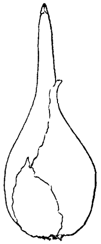

FIG. 4. — A galled fascicle sketched in July. Natural size.

To learn what plant tissues were affected, and in what manner, so that some conclusion might be drawn as to the immediate cause of the hypertrophy, there were selected for more careful study leaf bundles taken in April — the season of great changes and development in the leaf bundle. All of the material was fixed in hot alcoholic corrosive sublimate, a saturated solution in 30 per cent alcohol being used.

If a galled leaf bundle is examined in the middle of April or the first of May, the cavities in which the larvæ lie will be found almost completely developed. The cavity is in the axil of the leaf and is nearly covered above and on the sides by

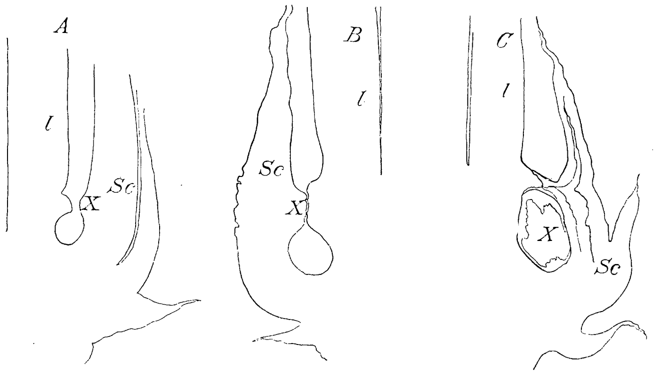

FIG. 5. — Showing the development of the protuberances which enclose the upper part of the larval cavity: *A*, May 1; *B*, July 15; *C*, mature, autumn (*l*, leaf; *Sc*, scale; *X*, development of protuberances and larval cavity). × 28½.

projections of plant tissue, one from the periphery of the leaf, and another from the inner surface of the inside scale (Fig. 5, *A*). It will be seen by consulting Fig. 6 that the young larvæ are at this time completely surrounded by thin-walled cells, and that the plant tissue which is in contact with the body of the parasite is composed of epidermis, thus showing that the parasite has consumed none of the plant cells or tissues.

The young epidermal cells of the young normal leaf are long, thin-walled, and have little granular contents. The older epidermal cells lose their contents, their outer walls become strongly cutinized, and they serve the plant only as a protective covering.

The epidermal cells of the leaf which are in contact with the larvæ have an appearance quite different from those epidermal cells in the other parts of the leaf. The first difference is noticed in the size and shape of the epidermal cells that line the cavity in which the larvæ lie. They are much longer and deeper than the normal epidermal cells, and they very closely resemble the cells lying beneath them, which are the large mesophyll cells. Furthermore, these epidermal cells are densely filled with granular food matter. Above the larval cavity, where the epidermal cells of the leaf arch over to meet those of the scale, they are shorter and deeper than those leaf epidermal cells touching the larvæ, but they are much larger than the epidermal cells in the older parts of the leaf into which they insensibly merge (Fig. 6). These cells have less contents than those in contact with the larvæ, but more, again, than the normal leaf epidermal cells.

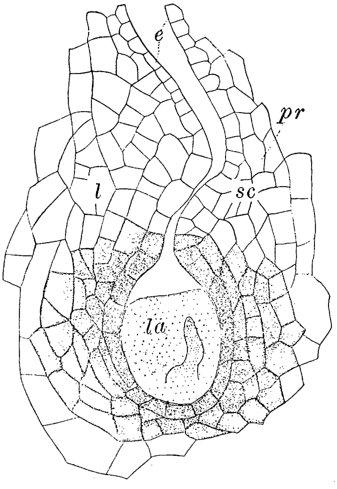

FIG. 6. — Longitudinal section through a cavity containing a young larva. The shaded area indicates the tissues with the densest cell contents (*la*, larva; *sc*, scale; *l*, leaf; *e*, epidermis; *pr*, parenchyma). April 25. × *circa* 56.

The epidermal cells on the inner surface of normal scales are long, shallow, and thin-walled; the epidermis on the outer surface varies only in the character of the outer cell wall, which, in this case, is thickened and strengthened by transverse ridges. On the inner surface and near the base of the scales the epidermal cells are shorter and resemble those of the leaf at a corresponding distance from the axis. The epidermal cells of the scales have very little contents.

In the galled leaves the scale epidermis lining the cavity in which the larvæ lie consists of long, thin-walled cells, which in size, shape, and density of contents resemble those epidermal cells of the leaf that line the other part of the cavity. The scale epidermal cells are shorter and deeper above the larvæ where the epidermis of the scale and of the leaf meet, and they gradually change into the normal form, somewhat above the neck of the larval cavity (Fig. 6).

It is thus seen that, in consequence of the presence of the parasite, the epidermis of scale and leaf is modified in shape and size, in structure, in contents, and in function.

A cross-section of the base of a galled leaf bundle, made from one of the same age as that represented in the longitudinal section in Fig. 6, shows that the tissue adjacent to the cavities containing larvæ is mainly parenchymatous, *i.e.*, the cells that compose it are relatively large and thin-walled, and are those cells which, in plants, are most sensitive to stimuli.

The tissue of the scale base is composed of large, rounded cells, between which are many intercellular spaces. These cells have but little contents. Near the juncture of scale base and leaf the cells are some of them larger and some smaller, and there are fewer intercellular spaces. In the axil of scale and leaf the cells are normally much smaller than any met with in the scale. Finally, the tissue surrounding the rudimentary conducting tissue, which in galled leaves abuts on the inside of the cavity containing the larvæ, is composed of small cells of the kind just described as occurring in the scale base. The thin-walled mesophyll cells of the leaf normally are differentiated into quite another tissue; as the leaf becomes older these cells become oblong, thick-walled, supporting cells (sclerenchyma) of the mature pine leaf. The cells of the tissues described have but little contents.

The parenchymatous tissue of the scale and leaf which is in contact with the epidermis of the cavity containing larvæ, for two or three cells from the cavity, follows the shape, size, and appearance of the epidermal cells (Fig. 6). Beyond these layers of parenchyma the cells become larger than in normal corresponding tissue, and gradually merge into the tissues of the scale on the one hand, and of the leaf on the other. These cells for six or eight layers around the cavity are filled with granular matter that increases in density toward the cavity.

The parenchymatous tissues which surround the parasite are affected in a negative manner as well. They are prevented from being differentiated and from developing as do their fellows under normal conditions. The scales in the normal leaf bundle turn brown early and die. They form the cup which surrounds the bases of the three leaves, or "needles," and which persists during the period of the normal leaf's activity. In the scales of the galled bundle the parenchymatous tissues remain active until early autumn, or during the activity of the parasite. Those cells of the leaf inside the region of the cavities containing larvæ, as has been stated, become in normal leaves thick-walled supporting tissue. In galled leaves they become, when fully developed, as large as the underlying parenchyma, and their walls in thickness reach a condition intermediate between the thick-walled supporting tissue, or sclerenchyma, and the parenchyma.

It is to the change in form and size of the cells which surround the cavity containing larvæ that the hypertrophy is due.

In July the condition of the galled leaf bundles of the Monterey pine differs only in degree from that just described as their condition in April. The parenchymatous cells are somewhat larger, the epidermis of the cavity containing larvæ, and all of the cells in the adjacent tissues of the scale and leaf, are active in providing food for the growing larvæ.

III.

We come now to the question, What is the immediate cause of the hypertrophy? And to this only an imperfect, and perhaps unsatisfactory, answer can be given. And this must be based on the all too slight evidence which lies before us.

There is no indication that the hypertrophy is either caused or affected by any substance deposited with the eggs.

Extensive experimentation would be necessary to prove what the effect would be of a foreign body, living or lifeless, in contact with such plant tissues; or, again, how much the waste matter given off from a living body would affect the tissues. There is some evidence, although negative, touching the former in the cases cited above, where the eggs of the gallfly were placed either between the scales or between the inside scale and near the tip of the leaf. In neither of these cases did the larvæ mature, and the reason for this must be that the cells which touched the young larvæ were not such as could easily give up their contents to nourish the parasite. In either case, however, they hatched into larvæ, and we may believe that, although no food may have passed from the cells of the host to the parasite, yet the plant tissues may have been mechanically irritated by the mere presence of a living foreign body. That the leaf epidermis was thickened would appear to make no difference if the plant tissues in question were stimulated to abnormal growth, mostly by this mechanical irritation, because cases are not wanting among plants[1] in which epidermal cells, although strongly cutinized, have been rejuvenated and have been caused to perform functions other than normal, or at least usual, and this, too, mainly from external mechanical stimulation. It is highly probable that the mere presence of the parasite does, to some extent, in the case of this gall, as in others, stimulate the living plant tissues.

Briefly it appears that the immediate and principal cause of the hypertrophy is the response on the part of certain plant tissues to the parasite's demand for food. This is indicated mainly by the gradual enlargement of the cells surrounding the parasite, in a manner which corresponds to its growth, and also by the unusual amount of food material which these cells contain.

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[1] Peirce, G. J. On the Structure of the Haustoria of Some Phanerogamic Parasites, *Annals of Botany*, vol. vii (1893), No. 27, p. 295.

IV.

I have been asked, why does not this gall attack other species of pine? and it may be said that one other species, of half a dozen that were examined which are growing in the Stanford University arboretum (*Pinus attenuata*), has a few galled leaf bundles. The young shoot of this pine is, early in the growing season, similar in structure and size to that of the Monterey pine, but the leaves of *P. attenuata* do not remain the right length for being visited by the gallfly long enough to be seriously injured by it. The other species of pine do not develop their shoots at the right time, or the shoots are covered with resin, or they are otherwise unfitted either by size or by structure to be galled. The opinion may be ventured that the conditions for the proper laying of the eggs and those governing the life of the larvæ are so delicate and exacting that other species of our pines are not likely to suffer from the parasite.

The materials for this paper were collected in the spring and summer of 1898, from galled Monterey pines which were growing in the university arboretum.

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